SEASONAL VARIATION IN AVIAN COMMUNITY COMPOSITION IN A HIGH-ANDEAN *POLYLEPIS* (ROSACEAE) FOREST FRAGMENT

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ABSTRACT.—We analyzed seasonal variation in avian species richness and relative abundance at the community and guild level during a 13-month period in central Bolivia in an 11-ha patch of *Polylepis* (Rosaceae) forest, a high-Andean ecosystem that has suffered from extreme anthropogenic fragmentation. Birds were surveyed audio-visually (supplemented with mist net data) and assigned to five relative abundance categories for 2-month survey periods. We recorded 35 core species, including 16 insectivores (46%), 11 frugi-granivores (31%), seven nectarivores (20%), and one carnivore (3%). Core species richness varied from 25 (June–July) to 33 (October–November). Insectivores had a significantly higher proportion of year-round residents (81%) than frugi-granivores (45%) or nectarivores (14%); the same trend was evident with respect to seasonal variation in species richness of each guild. Although most species varied considerably in their relative abundance, no guild showed significant variation in relative abundance scores among survey periods. However, frugi-granivores and nectarivores combined, both of which depend upon plants as food resources, reached a significant minimum in mid-winter (June–July), and the same result was found at the community level. The insectivore guild thus was the most temporally stable both in terms of species richness and abundance. Qualitative observations indicated that the fluctuations in frugi-granivores and nectarivores were related to the availability of food resources. *Received 22 April 2003, accepted 1 August 2003.*

Seasonal variation in the composition of Neotropical bird communities has been investigated in only a small number of case studies (Karr 1976, Brooks 1997, Hilty 1997, Schmitt et al. 1997). Such research often is hampered by high levels of Neotropical community diversity, a fairly large proportion of hard-to-detect cryptic or naturally rare species, and logistic constraints. These factors frequently impede the use of standard survey techniques and make it difficult to obtain sufficiently complete, comparable species inventories (Herzog et al. 2002a). Most studies on seasonal variation therefore have limited their scope to subsets of communities, such as hummingbirds (Stiles 1980, 1985a), understory frugivores (Loiselle and Blake 1991), mixed species flocks (Develey and Peres 2000), or canopy birds (Loiselle 1988).

Temporal variability in community structure is caused by local movements (Karr and Freemark 1983, Fjeldså 1991, Davis 1993), altitudinal migration (Stiles 1988, Loiselle and Blake 1991), or long distance latitudinal migration (e.g., Marantz and Remsen 1991, Davis 1993) of a considerable number of species. Movement and migration patterns have been hypothesized or documented to reflect food resource availability (Karr 1976, Stiles 1980, Loiselle 1988, Blake and Loiselle 1991, Loiselle and Blake 1991, Levey and Stiles 1992, Brooks 1997). Different food resources tend to show asynchronous abundance peaks (Karr 1976, Develey and Peres 2000), and different guilds therefore may be expected to show dissimilar patterns, but little data for within-community comparisons are available to test this prediction (but see Blake and Loiselle 1991).

Based on studies in lowland Panama, Karr (1976) hypothesized that in the tropics seasonal variability in diversity should increase from omnivores to frugivores to insectivores. This was supported by Brooks (1997), who found the highest seasonality for insectivores in the Paraguayan *chaco*. In Neotropical montane forests, however, most altitudinal migrants, which often comprise >30% of local avifaunas (Loiselle and Blake 1991), are frugivores or nectarivores (Stiles 1985b, Blake et

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al. 1990, Hilty 1997), and insectivore fluctuations therefore may have little impact on community composition in this habitat. Thus, studies in other habitats and biogeographic regions are required to determine general patterns and key factors determining the composition of tropical bird communities.

We analyzed seasonal variation in species richness and relative abundance at the community and guild level in a high-Andean *Polylepis* (Rosaceae) forest fragment during a 13-month period in central Bolivia. Specifically, we investigated whether seasonal changes in community richness and overall abundance occurred, and if insectivores showed more pronounced seasonality than other guilds in this marginally tropical, high-elevation forest ecosystem as proposed by Karr (1976) for the tropical lowlands. Since *Polylepis* forests have suffered from strong anthropogenic fragmentation (Fjeldså and Kessler 1996, Kessler 2002), we paid particular attention to abundance patterns of habitat specialists to assess implications for their conservation.

STUDY AREA AND METHODS

Study area.—We studied the bird community of an 11-ha fragment of *Polylepis besseri* forest located just north of the small community of Sacha Loma in the department of Cochabamba, Bolivia (17° 44′ S, 65° 34′ W, 3,710–3,880 m elevation) from November 1999 to November 2000. The fragment consisted of 9.3 ha of forest enclosing a 1.7-ha boulder field largely devoid of vegetation. Tree height varied from 4–10 m. Shrubs (*Gynoxis, Berberis, Ribes, Baccharis, Brachyotum*) were distributed patchily, and the ground largely was covered by bunch grass (*Festuca, Stipa, Calamagrostis*). Except for some densely vegetated spots, most of the vegetation was open enough to allow unobstructed passage on foot. Human impact on the forest (cattle grazing, fire wood cutting) was low, but the surrounding grassland was used intensively for sheep grazing. For a detailed description of the vegetation see Fernández et al. (2001).

The study site is embedded in a landscape mosaic of high-Andean *puna* grassland and more or less isolated *Polylepis besseri* fragments (varying in size from 0.01–100 ha) in

the transition zone from humid montane forests on the eastern Andean slope to dry intermontane valleys of southern Bolivia. The study fragment is 10 m from an about 40-ha forest patch with a considerably lower tree density and about 600 m from a 100-ha fragment with a similar vegetation structure. Climatic differences between seasons in the study area are pronounced. The rainy season (austral summer) extends from November to March, whereas dry conditions prevail from May to September during the austral winter. Brief transition periods occur in April and October. No climatic data are available for the study area, but Fernández et al. (2001) present temperature and precipitation values from two nearby climatic stations (Alalay, Toralapa) at elevations similar to that of the study fragment, however without stating the number of years of data. Mean annual precipitation at Alalay is 72 cm with a maximum of 17 cm in January. The five rainy season months combined receive over 60 cm of precipitation, whereas the five dry season months combined receive slightly less than 5 cm. Mean annual temperature at Toralapa is 8.7°C with monthly maxima of about 10–11° C in the rainy season, which drop to a minimum of about 7° C in June. Mean monthly minima drop to below freezing from April to October (with a minimum of about −5° C in June and July) and remain slightly above 0°C during the rainy season.

Field surveys.—We surveyed the *Polylepis* bird community for several days each month except in February and March 2000, when social unrest did not allow field work in Sacha Loma. Survey dates were 10–12 November and 7–12 December 1999, 27–31 January, 13–18 April, 10–13 and 24–29 May, 11–13 June, 2–4 and 9–11 July, 3–7 August, 15–17 September, 14–16 and 22–24 October, and 13–17 November 2000. SKH and RSA determined the presence and relative abundance of bird species by daily walks through the fragment during most of the daylight period, and we monitored vocal activity of nocturnal species from our camp site near the forest edge. We identified birds both visually and acoustically, and SKH was familiar with sight and sound identification of all species before beginning data collection. Also, we operated 10–15 mist nets daily during the same visits starting in

December 1999 (see Herzog et al. 2002b). We used intensive observations of foraging behavior (e.g., mixed species foraging flocks; Herzog et al. 2002b) and opportunistic examination of fecal material (mainly during handling of netted birds, rarely upon encounter in the forest; fecal matter was screened for presence of fruit pulp, seed remnants, or chitinous insect parts) to determine the primary diet of each species in the study area. For some species we also consulted standard references (e.g., Fjeldså and Krabbe 1990).

As some species and many individuals remained unmarked even after several months of banding operations, and because thorough spot map surveys of all species were unfeasible due to time constraints, we estimated relative rather than absolute abundances of species for each month based on the frequency of encounter of a given species. We distinguished five relative abundance categories: (a) rare, no more than three observations of single individuals or one observation each of a pair and a single bird, suggesting that no more than two to three individuals may have been present; (b) uncommon, single individuals or pairs observed occasionally but not daily, probably four to six individuals present; (c) fairly common, small numbers observed daily or almost daily, probably 7–12 individuals present; (d) common, observed repeatedly every day, probably 13–20 individuals present; and (e) abundant, observed daily in large numbers, >20 individuals present. Due to the biases of mist net capture data (e.g., Remsen and Good 1996), relative abundance estimates were based almost exclusively on visual and acoustical observations. For rare and uncommon species, we consulted data from mist net captures, and in a few cases we increased a species' relative abundance by one rank when mist net data indicated a slightly higher abundance than observational data.

Data analysis.—We included only core species (those that regularly breed, winter, or migrate through a given habitat; Remsen 1994) of the *Polylepis* fragment in the present analysis. Species considered rare visitors from nearby habitats, dispersing individuals, or vagrants were not analyzed. Valid, meaningful comparisons of community composition within or between sites require similar levels of sampling effort and survey completeness

(Remsen 1994). Because survey effort varied among months, we combined monthly data into five 2-month periods based on climatic and biological characteristics: December–January (11 survey days), April–May (16), June–July (9), August–September (8), and October–November (14). December and January are the two months of greatest precipitation (Fernández et al. 2001) and correspond to the late breeding season for most *Polylepis* species (authors pers. obs.). April and May represent the transition period from the rainy to the dry season, whereas June and July are characterized by the lowest temperature and precipitation values (Fernández et al. 2001). The onset of territorial behavior in several core species occurs in August and September (Herzog et al. 2002b), followed by the peak of the breeding season for most *Polylepis* species (see Fjeldså and Krabbe 1990; authors pers. obs.) and the transition period from the dry to the rainy season in October and November.

Taking into account the small size of the forest fragment, its open vegetation structure, and relatively low species richness, as well as SKH's familiarity with the avifauna, we consider that despite the differences in survey effort >95% of all core species were recorded in each 2-month period (see also Fjeldså 1993 for an assessment of minimum survey effort in *Polylepis* woodlands). Although the April–May period received the highest survey effort, six days of field work during late May added only a single core species that had not been recorded during April or early May. This indicates that our assumption of >95% completeness in all periods is warranted.

We assigned all core species to one of four primary diet categories: insectivores (species that primarily consume insects and other arthropods), frugi-granivores (species that primarily consume fruit, seeds, and flowers), nectarivores (species that primarily consume nectar), and carnivores (species that primarily consume vertebrate prey). We ranked relative abundance categories on an ordinal scale of increasing abundance from 0 (not recorded) to 5 (abundant). If a species' abundance varied between months within the same 2-month period, the mean was used (e.g., 2.5 for a species uncommon in June and fairly common in July). However, a species that was rare in one month and not recorded in the other month of

a given 2-month period was still considered rare and assigned an abundance rank of 1.

We performed sign tests to analyze changes in relative abundance within guilds and for the entire bird community between consecutive 2-month periods using STATISTICA for Windows (StatSoft, Inc. 1997). We examined differences among guilds in the proportion of year-round residents with a Fisher exact test using StatXact (Cytel Software Corp. 1995).

RESULTS

Species richness.—We recorded a total of 35 core species, including 16 insectivores (46%), 11 frugi-granivores (31%), 7 nectarivores (20%), and 1 carnivore (3%; Table 1). An additional 25 vagrant or visiting species were observed in the study site (Appendix). Nineteen (54%) core species were year-round residents (i.e., they were recorded during all 2-month periods), whereas three core species (9%) each were observed during only one period. Among insectivores, 13 species (81%) were year-round residents, whereas only 5 frugi-granivores (45%) and 1 nectarivore (14%) were recorded during all periods. These differences in the proportion of year-round residents among guilds were significant (Fisher exact test, $P = 0.008$). The single carnivore, the Yungas Pygmy-Owl (*Glaucidium bolivianum*), was observed during all periods except December–January, but it may have been overlooked then due to its crepuscular and nocturnal activity.

Core species richness of the *Polylepis* bird community was lowest in winter, with 25 species during June–July and 26 species during August–September, and it was highest during the two transition periods, with 29 species during April–May and 33 species during October–November (Fig. 1A). The latter two months correspond to the height of the breeding season of most *Polylepis* birds (authors pers. obs.; see Fjeldså and Krabbe 1990). During December–January, species richness was slightly higher (27 species) than during winter. Insectivore richness showed low variability among periods, varying from 13 species during December–January to 16 species during October–November. In contrast, nectarivore richness was twice as high during April–May (six species) and more than twice as high during October–November (seven species) than

during the periods from June through September (three species). Variability in frugi-granivore richness was intermediate with a minimum of six species during June–July and maxima of nine species during April–May and October–November (Fig. 1A).

Relative abundance.—Most species varied considerably in their relative abundance, the extreme case being the Sparkling Violetear (*Colibri coruscans*), which was common during December but absent from June through September (Table 1). Of the 19 year-round residents, 11 varied in their abundance by more than one category (Table 1). Thus, only eight species (23% of the entire core community) were fairly constant year round.

Overall abundance at the community level peaked during October–November (sum of abundance scores 75.0, mean 2.3) and was lowest during June–July (47.0, 1.9), and we found similar patterns at the guild level (Fig. 1B). When comparing species abundance scores between consecutive periods, none of the three guilds analyzed alone showed any significant variation (Table 2, results shown for insectivores only). Because frugi-granivores and nectarivores both depend upon plants as food resources, we pooled the data for the two guilds, which revealed a significant decrease from April–May to June–July ($Z = 2.41$, df = 15, $P = 0.016$) and a significant increase from June–July to August–September ($Z = 2.02$, df = 11, $P = 0.043$) in abundance (Table 2). We obtained similar results for the entire bird community, except that the decrease in abundance from October–November to December–January also was significant (Table 2). Note that we compared December–January to October–November of the next year, assuming between-year continuity.

Habitat specialists.—Three core species, the Tawny Tit-Spinetail (*Leptasthenura yanacensis*), the Giant Conebill (*Oreomanes fraseri*), and the Thick-billed Siskin (*Carduelis crassirostris*) are strongly specialized on *Polylepis* forest, and five species (Rusty-vented Canastero, *Asthenes dorbignyi*; Streak-fronted Thornbird, *Phacellodomus striaticeps*; Rufous-webbed Bush-Tyrant, *Polioxolmis rufipennis*; D'Orbigny's Chat-Tyrant, *Ochthoeca oenanthoides*; Rufous-bellied Saltator, *Saltator rufiventris*) show a marked affinity for this habitat (see Fjeldså and Kessler 1996). The

TABLE 1. Most of the 35 core species recorded in a *Polylepis* woodland at Sacha Loma, central Bolivia, varied in relative abundance (n.r. = not recorded; R = rare; U = uncommon; F = fairly common; C = common; A = abundant; see text for details) between 2-month survey periods, November 1999 to November 2000. At the guild level (ins = insectivore; fru = frugi-granivore; nec = nectarivore; car = carnivore), most insectivores were year-round residents, whereas the reverse was true for frugi-granivores and nectarivores. No data were collected in February and March. Taxonomy follows South American Checklist Committee (2002).

Species	Survey period					Diet
	Dec–Jan	Apr–May	June–July	Aug–Sept	Oct–Nov	
Ornate Tinamou (*Nothoprocta ornata*)	R	R	U-R	U	R	fru
Spot-winged Pigeon (*Columba maculosa*)	R	U	U-R	U	R	fru
Gray-hooded Parakeet (*Psilopsiagon aymara*)	R	n.r.	n.r.	n.r.	n.r.-U	fru
Yungas Pygmy-Owl (*Glaucidium bolivianum*)	n.r.	R	R	U	R	car
Sparkling Violetear (*Colibri coruscans*)	C-R	R	n.r.	n.r.	R	nec
Black-hooded Sunbeam (*Aglaeactis pamela*)	R	R	n.r.	n.r.	R	nec
Andean Hillstar (*Oreotrochilus estella*)	n.r.	R-U	R-U	F	U-R	nec
White-sided Hillstar (*O. leucopleurus*)	n.r.	n.r.	n.r.	R-U	U-n.r.	nec
Giant Hummingbird (*Patagona gigas*)	R	R	R	n.r.	R	nec
Red-tailed Comet (*Sappho sparganura*)	R	R	n.r.	n.r.	U	nec
Plain-breasted Earthcreeper (*Upucerthia jelskii*)	R	R-U	R	R	R	ins
Bar-winged Cinclodes (*Cinclodes fuscus*)	C	C-R	R	R	F-C	ins
Brown-capped Tit-Spinetail (*Leptasthenura fuliginiceps*)	n.r.	n.r.	n.r.	n.r.	R-U	ins
Tawny Tit-Spinetail (*L. yanacensis*)	C	C	C	C	C	ins
Cordilleran Canastero (*Asthenes modesta*)	R	n.r.	R	R	R-n.r.	ins
Rusty-vented Canastero (*A. dorbignyi*)	C	C-F	F	F	C	ins
Puna Canastero (*A. sclateri*)	F	U	R	F	F	ins
Streak-fronted Thornbird (*Phacellodomus striaticeps*)	F	C-F	U	U	F	ins
Puna Tapaculo (*Scytalopus simonsi*)	C	F	U	U	F-C	ins
White-throated Tyrannulet (*Mecocerculus leucophrys*)	U	R-F	F	F	F	ins
Tufted Tit-Tyrant (*Anairetes parulus*)	R	U	U-F	U	R	ins
Rufous-webbed Bush-Tyrant (*Polioxolmis rufipennis*)	F-U	C-U	U-R	U	F	ins
D'Orbigny's Chat-Tyrant (*Ochthoeca oenanthoides*)	R	F	F	F	U	ins
White-browed Chat-Tyrant (*O. leucophrys*)	F	R	R	U	F-C	ins
Red-crested Cotinga (*Ampelion rubrocristatus*)	n.r.	U-n.r.	n.r.	n.r.	n.r.	fru
Andean Swallow (*Haplochelidon andecola*)	n.r.	n.r.	R-U	R	R-U	ins
Chiguanco Thrush (*Turdus chiguanco*)	U	C-F	U-F	F	F-C	fru
Giant Conebill (*Oreomanes fraseri*)	F	F	F	F	F	ins
Gray-bellied Flowerpiercer (*Diglossa carbonaria*)	F	n.r.-U	R	U	F-C	nec
Common Bush-Tanager (*Chlorospingus ophthalmicus*)	n.r.	n.r.	n.r.	n.r.	R	fru
Rufous-collared Sparrow (*Zonotrichia capensis*)	A-C	C-F	U-R	F	A	fru
Ash-breasted Sierra-Finch (*Phrygilus plebejus*)	A-C	C	C	A	A	fru
Rufous-bellied Saltator (*Saltator rufiventris*)	n.r.	R	R	n.r.	n.r.	fru
Thick-billed Siskin (*Carduelis crassirostris*)	U-F	R	n.r.	F	U-F	fru
Hooded Siskin (*C. magellanica*)	C	U-n.r.	n.r.	R	n.r.-F	fru

Tawny Tit-Spinetail and the Giant Conebill had constant abundance year round (Table 1). The Rusty-vented Canastero and the Streak-fronted Thornbird showed slight variation, being least abundant during the austral winter, whereas the D'Orbigny's Chat-Tyrant had its lowest abundance during December–January, and the Rufous-webbed Bush-Tyrant lacked a clear pattern. The Thick-billed Siskin was not recorded during June–July and peaked in abundance from August through January. The

Rufous-bellied Saltator was recorded only during April–May and June–July when it was rare.

Noteworthy distributional record.—The occurrence of the White-sided Hillstar (*Oreotrochilus leucopleurus*) at Sacha Loma during the austral winter (Table 1) represents a northward range extension by about 400 km for this Andean species, which breeds mainly in Argentina and Chile and previously was known only from as far north as the department of Tarija
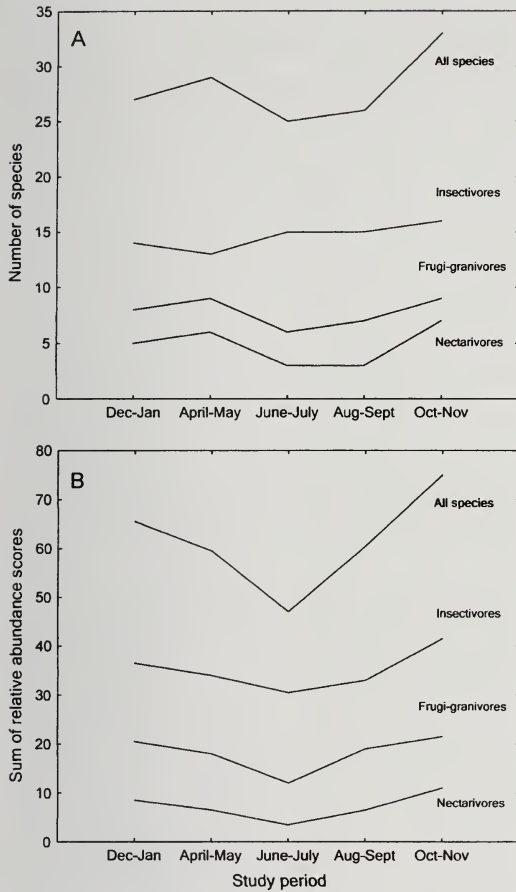
FIG. 1. Insectivores were the most temporally stable guild in the *Polylepis* bird community at Sacha Loma, central Bolivia, from November 1999 to November 2000, both in terms of (A) species richness and (B) relative abundance. No data were collected in February and March.

in southern Bolivia (Fjeldså and Krabbe 1990, Arribas et al. 1995, Fjeldså 1999). We first mist netted a male on 9 June 2000 in a nearby *Polylepis* patch, followed by a capture of a male on 7 August 2000 and subsequent observations until 16 October 2000 in the study fragment. Males of the White-sided Hillstar differ from those of the sympatric central Bolivian subspecies of the Andean Hillstar (*O. estella boliviana*) primarily by their blue-black rather than chestnut median stripe on the underparts (Fjeldså and Krabbe 1990).

These observations represent the first evidence that the White-sided Hillstar is an austral migrant. Although Marín et al. (1989) suggested that Chilean birds might migrate based on a single record in southern Antofagasta, de la Peña (1994) and Fjeldså (1999) mentioned only altitudinal movements for the species, and Parker et al. (1996) did not list the White-sided Hillstar as an austral migrant.

DISCUSSION

The insectivore guild was the most temporally stable at Sacha Loma both in terms of species richness and abundance, and we found no significant changes in abundance between seasons. In contrast, frugi-granivores and nectarivores combined showed considerable seasonal variation with a significant abundance low during the austral winter (June–July). Thus, our results indicate that Karr's (1976) hypothesis of highest seasonality in insectivores, which was derived from studies in tropical lowlands, does not apply to marginally tropical, high-elevation *Polylepis* forests. Seasonal variation at the community level largely reflected that of frugi-granivores and nectari-

TABLE 2. Frugi-granivores and nectarivores combined had a significantly low abundance in mid-winter (June–July) in a *Polylepis* woodland at Sacha Loma, central Bolivia, November 1999 to November 2000, as revealed by binomial sign tests comparing relative abundance scores between 2-month periods. This is reflected at the community level, whereas insectivores lacked significant variation. No data were collected in February and March.

Comparison	Insectivores ($n = 16$)		Frugi-granivores and nectarivores ($n = 18$)		All species ($n = 35$)	
	Z	P	Z	P	Z	P
Dec–Jan to April–May	0.0	1.000	0.29	0.773	0.20	0.838
April–May to June–July	0.60	0.546	2.41	0.016	2.35	0.019
June–July to Aug–Sept	0.0	1.000	2.02	0.043	2.12	0.034
Aug–Sept to Oct–Nov	1.58	0.114	1.03	0.302	1.54	0.124
Oct–Nov to Dec–Jan	1.06	0.289	1.58	0.114	2.01	0.044

vores, i.e., the two guilds dependent upon plants as food resources. The Sacha Loma bird community may be characterized as highly seasonal since only about one quarter of its core species were year-round residents with fairly constant abundances.

Relative abundance values do not necessarily reflect true abundances of species, but may be influenced by interspecific differences and seasonal changes in detectability. In the Bolivian Andes, vocal activity (and thus detectability) levels of forest birds tend to decrease considerably during the late rainy and first half of the dry season (SKH pers. obs.). Therefore, the question arises to what degree our data are biased by varying detectabilities of species. The relatively open vegetation structure of the *Polylepis* forest certainly reduced such biases, but even so, visually inconspicuous species that prefer to stay in dense vegetation or close to the ground, i.e., Ornate Tinamou (*Nothoprocta ornata*), Cordilleran (*Asthenes modesta*) and Puna (*A. sclateri*) canasteros, Puna Tapaculo (*Scytalopus simonsi*), and White-browed Chat-Tyrant (*O. leucophrys*), probably became less detectable during the late rainy season. The apparently low abundance of the Puna Tapaculo, a highly sedentary and almost flightless species (Fjeldså and Krabbe 1990), during the austral winter almost certainly is a result of reduced vocal activity during that season. However, except for the Ornate Tinamou, these visually cryptic species are insectivores. Thus, if seasonal changes in detectability biased our data, one would expect to find pronounced seasonal variation in abundance for insectivores rather than for frugi-granivores and nectarivores, which was not the case in Sacha Loma. In fact, the true seasonality in insectivores compared to frugi-granivores and nectarivores therefore is likely to be even less than what Fig. 1 indicates.

Several studies have shown that variations in abundance of birds over time are related to the availability of food resources (Karr 1976, Blake and Loiselle 1991, Loiselle and Blake 1991, Levey and Stiles 1992, Strong and Johnson 2001). Although we lack quantitative data on food supply, some comparisons can be made based on qualitative observations. Flowering and seeding of *Polylepis* trees, for example, is strictly seasonal. The first *Poly-lepis* trees had open flowers during July, and most trees were flowering during early August. Seeds still were present during late January and extended into February, but none were observed during mid-April. This pattern largely coincided with the abundance fluctuations of the Thick-billed Siskin, a habitat specialist that mainly feeds on flowers and seeds of *Polylepis* (Fjeldså and Krabbe 1990, Herzog et al. 2001). Other common woody plants such as *Berberis* (Berberidaceae) also started flowering during August, producing fruits and seeds during the rainy season.

Nectarivores primarily were observed at the flowers of two species, the annual vine *Salpichroa glandulosa* (Solanaceae) and the mistletoe *Tristerix penduliflorus* (Loranthaceae), a hemiparasite on *Polylepis* trees, although they also used other, less conspicuous flowers. Whereas *S. glandulosa* flowering was restricted to the rainy season, mistletoe flowers (and fruit) were available year round, but had their lowest abundance during the middle of the austral winter when species richness and abundance of nectarivores also was lowest. It is noteworthy that the Gray-bellied Flowerpiercer (*Diglossa carbonaria*) was the only nectarivore with year-round presence at Sacha Loma. This possibly was due to the feeding method of flowerpiercers, resulting in less specialization and allowing them to use a greater variety of flowers than any of the hummingbird species (Naoki 1998). Alternatively, *D. carbonaria* may have shifted to a more insectivorous diet during the dry season, given that Isler and Isler (1999) reported insect parts as stomach contents for this species.

Although the insectivore guild did not show significant abundance fluctuations, some insectivorous species nonetheless changed in abundance possibly in response to a variable food supply. The Bar-winged Cinclodes (*Cinclodes fuscus*) mostly forages along streams, on wet bogs or grassy glades, often in *Polylepis* woodlands (Fjeldså and Krabbe 1990, Fjeldså and Kessler 1996). This species was common during the rainy season when ephemeral aquatic microhabitats formed frequently, both in the *Polylepis* woodland and in the surrounding *puna* grassland, whereas it was rare during the dry season when even some springs near Sacha Loma dried up. This pattern coincides with anecdotal observations

of drastic body mass decrease in two banded *C. fuscus* individuals. When banded at the beginning of the dry season on 10 May 2000, the first bird had a body mass of 27.0 g and showed no traces of subcutaneous fat. The same bird was recaptured during the height of the dry season on 5 August 2000 weighing 20.5 g, 74% of its body mass in May. A second bird decreased in body mass from 31.5 g (again without signs of subcutaneous fat deposits) on 28 January 2000 to 27.0 g on 13 October 2000, suggesting that it reached a minimum during the dry season. Although we can not dismiss the possibility that those body mass losses were caused by other factors (e.g., a heavy parasite load), the most plausible explanation is a strong reduction in food supply and optimal foraging habitat during the dry season.

Of the eight *Polylepis* specialists recorded at Sacha Loma, six species showed variations in abundance, two of which left the fragment during part of the year. Those six species probably depend upon a certain degree of connectivity between suitable habitat patches, especially when inhabiting small fragments with more homogeneous environmental conditions than larger patches that cover greater elevational gradients. The need for habitat connectivity also might apply to some extent to the Giant Conebill, which, despite constant abundance during the study period, exhibited movements between fragments at Sacha Loma (Herzog et al. 2002b). Because anthropogenic fragmentation and deforestation of *Polylepis* woodlands due to excessive burning and grazing are ongoing (Fjeldså and Kessler 1996, Fjeldså 2002, Hensen 2002), studies on the metapopulation dynamics of *Polylepis* specialists are urgently needed to determine how they respond to such disturbance.

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APPENDIX

Differentiating between core species and visitors or vagrants is not always a straightforward process and may be disputable in some cases. Thus, we present a commented list of all species observed in the forest, directly at its edge, or flying over that were not considered core species of the *Polylepis* fragment at Sacha Loma, central Bolivia. Species exclusively observed in the surrounding *puna* grassland are not included.

Darwin's Nothura (*Nothura darwinii*). Observed only once during October 2000, when several birds were heard at forest edge.

Turkey Vulture (*Cathartes aura*). Single birds flying over the forest and *puna* during April, May, and August 2000.

Andean Condor (*Vultur gryphus*). Rare sightings of soaring birds during April, May, and July 2000.

Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*). Observed only during August 2000 in flight.

Red-backed Hawk (*Buteo polyosoma*). Seen in small numbers during most months in flight

or on ground in *puna* grassland. This species potentially may hunt in the forest fragment, but we never observed this behavior.

Mountain Caracara (*Phalcoboenus megalopterus*). This common *puna* species was observed in flight and on the ground in *puna* during most months.

Aplomado Falcon (*Falco femoralis*). We observed two birds hunting a passerine over *puna* during December 1999, and single birds were seen once each during May, June, July, and August 2000 either perched on top of a *Polylepis* tree or hovering over the fragment. This species may very occasionally prey on a *Polylepis* bird, but this alone does not warrant inclusion as a core species.

Blue-crowned Parakeet (*Aratinga acuticaudata*). We saw a flock of eight birds once during October 2000 in fast flight over the fragment.

Mitred Parakeet (*Aratinga mitrata*). We saw a flock of 8–10 birds once during December 1999 in fast flight over the fragment.

Mountain Parakeet (*Psilopsiagon aurifrons*). Small flocks in fast flight observed during May, July, August, and October 2000, but never observed perched in the forest.

White-collared Swift (*Streptoprocne zonaris*). A single bird circling relatively high above the forest in a flock together with the two *Aeronautes* species below during April 2000.

Andean Swift (*Aeronautes andecolus*). See White-tipped Swift (below).

White-tipped Swift (*Aeronautes montivagus*). A flock of about 50 birds circling together with two White-collared Swifts and about 50 Andean Swifts relatively high above the forest during April 2000.

White-vented Violet-ear (*Colibri serrirostris*). A single bird in pale juvenal plumage seen once during November 1999.

Great Sapphirewing (*Pterophanes cyanopterus*). Single birds seen twice in the forest during October 2000. Probably a rare visitor from the humid treeline zone.

Green-barred Woodpecker (*Colaptes melanochloros*). Two single birds observed during October 2000. Probably a rare visitor from deciduous forest at lower elevations.

Andean Flicker (*Colaptes rupicola*). Uncommon to common almost year-round (not recorded during June 2000) in the surrounding *puna* grassland, we observed this species only twice in the fragment, once at the edge (a copulating pair during November 1999) and once in the boulder field.

Rufous Casiornis (*Casiornis rufa*). We mist netted a single bird during August 2000. Probably a vagrant from deciduous forest at lower elevations.

Fawn-breasted Tanager (*Pipraeidea melanonota*). We mist netted a single bird during August 2000 and observed another during November 2000. Probably a vagrant.

Cinereous Conebill (*Conirostrum cinereum*). Two single birds seen during October 2000. This species regularly inhabits *Polylepis* forests and may form part of the core species community in some years.

Plumbeous Sierra-Finch (*Phrygilus unicolor*). We mist netted a single bird during April 2000. Surprisingly, we did not observe this species in the *puna* grassland around our study site.

Rufous-sided Warbling-Finch (*Poospiza hypochondria*). Sightings of one (dispersing?) bird in juvenal plumage during May 2000 and of two individuals in adult plumage during October 2000. This species regularly inhabits *Polylepis* forests and may form part of the core species community in some years.

Plain-colored Seedeater (*Catamenia inornata*). We mist netted a single bird during December 1999. This species regularly inhabits *Polylepis* forests and may form part of the core species community in some years.

Golden-billed Saltator (*Saltator aurantiirostris*). A single bird heard once during November 1999. Probably a rare visitor from deciduous scrub and gardens near houses at lower elevations.

Black Siskin (*Carduelis atrata*). Four birds moving through scattered *Polylepis* bushes at the fragment edge during April 2000. Probably a rare visitor.